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A BIOGEOGRAPHIC ACCOUNT OF THE GRASSHOPPERS (ORTHOPTERA: ACRIDOIDEA) OF SULAWESI, INDONESIA

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Nineteen acridid species were collected from the Dumoga Bone National Park and its environs in North Sulawesi, Indonesia, during 1985: two were new to science and one was known previously only from the Philippines.

The total acridoid fauna of Sulawesi, including these three species, comprises 61 species of Acrididae (53 Catantopinae, four Oedipodinae, three Acridinae, one Gomphocerinae) and one species of Pyrgomorphidae. This fauna has four main characteristics: (a) a high level of specific and generic-level endemism, (b) low generic-level diversity but a high number of species per genus, (c) diverse distributions outside Sulawesi, and (d) localised distributions within the island.

In the Catantopinae, 83% of species are endemic to Sulawesi, reflecting the importance of the island as an area of endemism. Species distributions within Sulawesi suggest that each region of the island (North, Central, South and South-east) may also be an area of endemism in its own right.

These observations are discussed in relation to the geological history of Sulawesi. They suggest that for much of its history the island has been more isolated from other land masses than it is at present, and that it has been fragmented either into separate islands or by ecological barriers.

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INTRODUCTION

Although the Acridoidea in temperate zones and in dry equatorial areas are well-known, only wide ranging, economically-important pests, e.g. *Oxya japonica japonica* Thunberg and *Locusta migratoria* Linnaeus, have been studied in wet equatorial areas. The taxonomic work in South-east Asia by Ramme (1941) and Willemse (1951, 1956, 1957) is an exception but it has not been extended. In particular, the acridoid fauna of Sulawesi has been largely ignored despite the great interest in other animal groups inhabiting the island.

Sulawesi lies in a deep sea region, also including the Lesser Sunda Islands (Lombok to Timor) and the Moluccas, with lies between two continental margins: the Sunda (Malaysia and the Greater Sunda Islands), and the Sahul shelves (New Guinea and offshore islands). Classically, this area was seen as the meeting point of two major biotas: the Oriental and the Australasian. Wallace (1869) originally separated them by dividing Bali (and Borneo) from Lombok (and Sulawesi). Although Wallace's Line may apply to some groups such as freshwater fish and mammals, the diversity of biogeographical patterns across this region for different taxonomic groups is high (see George 1987). Even with this overlap of broad transitional zones, Wallacea (a collective term for the islands of the deep sea region) is generally considered to be insular and biotically impoverished, but with unique characteristics indicating long periods of isolation (Dickerson et al. 1928).

Sulawesi covers 159,000 km² divided into four regions, Utara, Tengah, Selatan, and Tenggara, or North, Central, South, and South-east Sulawesi, respectively (see Whitten, Mustafa & Henderson 1987, for geographical details). North Sulawesi is a narrow peninsula, 772 by 103 km. Volcanoes, 1800-2400 m above sea level (asl), range along the peninsula. Seismic activity was recorded during 1985 and

1986. Limestone outcrops (possibly Cretaceous) oc-
cur in the western half of North Sulawesi. The
northern peninsula is linked with Central Sulawesi
by a narrow neck of land at the western extremity.
The Sangihe and Talaud Islands lie between the
northern tip of North Sulawesi and the Philippines.
Central Sulawesi is also mountainous, with peaks
reaching 2000-3000 m asl. A limestone mountain
range running north to south through South Su-
lawesi is 500-1000 m asl and bisected by a narrow
plain. The lakes on the plain are only 1-2 m deep
and were once part of the sea, suggesting that at
least this peninsula may have been partially sub-
merged at times. The single volcano in this region,
Lompobatang (2871 m asl), is extinct. The penin-
sula of South-east Sulawesi has a western mountain
range reaching 2800 m asl and a lower-lying eastern
area.

The vegetation is affected by regional climatic
differences. Central Sulawesi has the greatest ratio
of wet to dry months, whereas more seasonal rain-
fall occurs in the peninsulas (Whitmore 1984). The
central region is covered in evergreen rain forest,
whereas semideciduous forest is more common in
the peninsulas (Walker 1982). Open habitats are
mainly secondary, due to forest clearance for agri-
culture (Whitten et al. 1987).

Geologically Wallacea is a highly complex region
originating in an interaction between the South-
east Asian, Australian, and Pacific plates (Charlton
1986). The present island of Sulawesi is believed to
be derived from two fragments that originated se-
parately during the breakup of east Gondwanaland
about 320 My ago, and remained separate during a
northerly move starting 220 My ago (Audley-
Charles 1987). From the late Cretaceous onwards,
these fragments probably formed part of an ar-
chipelago between the Asian mainland and Austra-
lia-New Guinea but their positions relative to other
land masses are uncertain. Holloway (1987) em-
phasized two alternative theories about the rela-
tionship of Sulawesi with Borneo: 1. The fragment
now forming the western part of the island (North,
South and part of Central Sulawesi) has always been
in about its present position relative to Borneo,
whereas the eastern fragment was Australasian in
origin, 2. The two fragments were both isolated
island arcs, now fused and thrusted towards Borneo.
The present island was probably formed about 15
My ago. The area of land above sea level, its division
into separate islands and its climate are additional
factors which must have contributed to the present
day fauna of Sulawesi but about which little is
known (Morley & Flenley 1987).

It is now believed that Sulawesi was never linked
by land bridges to any other land mass following its
formation 15 My ago (Audley-Charles 1987; Hollo-
way 1987). During the Pleistocene, the sea level fell
several times when affected by the Glacial expan-
sion of the ice caps. The largest drop, 170,000 years
ago, linked Sundaland (Sumatra, Java, Bali, and Bor-
neo) with the Asian mainland, with land extensions
northward to the Philippines. Exposed land also
extended around South Sulawesi toward the Lesser
Sunda Islands, and from Central Sulawesi eastward
toward New Guinea. During these periods of low
sea level a drier, more seasonal climate prevailed
and dry savannah may have extended through the
Philippines to the Lesser Sunda Islands and into
Australia, separating two large, wet rainforest areas
in Sundaland and New Guinea; some seasonal
plants still survive in South Sulawesi (van Steenis
1979). The climatic fluctuations and corresponding
vegetational changes of the Quaternary are now
known to have occurred in the late Tertiary as well
(Morley & Flenley 1987).

Materials and methods

The analysis reported here is based on a combi-
nation of data from the literature and collections
made by the authors and others in the Dumoga-
Bone National Park, North Sulawesi during 1985.
This work formed part of the Royal Entomological
Society's 'Project Wallace' expedition. Insects were
collected by sweeping, beating, and hand-searching.
Agricultural crops, grassland, and primary semi-
deciduous forest (undergrowth, bushes, saplings,
and trees up to 2 m) were examined at all times of
day and night and in three separate periods cover-
ing most of the year. Specimens collected from the
tree canopy during the British Museum (Natural
History) fogging programme (N. Stork, unpub-
lished) were also examined.

The principal published records of the acridid
fauna of Sulawesi are: Ramme (1941), Dirsh
(1954), Willemse (1951, 1956, 1957, 1968), Hollis
(1968, 1971, 1975), Kevan & Chen (1969), and
Ritchie (1982). Family and subfamily classification
follows that adopted in the collection of the British
Museum (Natural History).

Results

Expedition collection of North Sulawesi
Acridoidea

Nineteen species from eighteen genera of Acri-
doidea were found in the Dumoga Bone National
Park and its environs during 1985 (table 1). This
includes two undescribed catantopine species, from
the genera *Tarbaleus* and *Bibracte*, both of which
were collected from the canopy by fogging. One
species, *Eoscyllina luzonica*, was previously known
only from the Philippines and was collected only
from limestone grassland in the western part of the
National Park. This suggests that the data available
in the literature on the species present in Sulawesi

Table 1. Species of Acridoidea occurring in Sulawesi and their distributions.

		Wings[1]		Distribution[2]		
				Outside	Within	
Pyrgomorphidae						
Atractomorpha				Across		
	psittacina psittacina de Haan	+	W	S, P	All	
Acrididae						
Acridinae						
Acrida				Across		
	willemsei Dirsh	+	W	S, P	All	
Calliphlaeoba				Sulawesi		
	celebensis Ramme	+	B	—	N, C	
Phlaeobacris				Sulawesi		
	reticulata Willemse		W	—	C	
Gomphocerinae						
Eoscyllina				P		
	luzonica Bolivar I	+	W	P	N	*
Oedipodinae						
Heteropternis				Across		
	obscurella Blanchard	+	W	Across	All	
Aiolopus				Across		
	thalassinus tamulus Fabricius	+	W	Across	All	
Locusta				Across		
	migratoria Linnaeus	+	W	Across	All	
Gastrimargus				Across		
	marmoratus (Thunberg)		W	Across	All	
Catantopinae – Endemic genera						
Alectorolophus	*deceptor* Ramme	+	B	—	SE, N	*
	obscoenus Brunner von Wattenwyl	+	B	—	N	*
	unilobatus Brunner von Wattenwyl		B	—	S	*
	applicatus Brunner von Wattenwyl		B	—	S, C	*
	speciosus Brunner von Wattenwyl		B	—	S	
	mutator Ramme		B	—	N	*
	sororum Ramme		B	—	C	*
	lineatus Ramme		B	—	C	*
	guttulosus Ramme		B	—	N	*
Acrolophus	*cornutus* Ramme		B	—	C	*
Alectorolophellus	*heinrichi* Ramme		B	—	S	*
Mengkokacris	*olivacea* Ramme		W?	—	SE	*
Heinrichius	*nobilis* Ramme		W	—	N	*
Celebesia	*acuticerca* Bolivar C	+	W?	—	N	*
	ferruginata Brunner von Wattenwyl		W?	—	N	*
	heinrichi Ramme		W?	—	S	*
Paramesambria	*flavomaculata* Willemse		B	—	S	*
Paracranae	*celebesia* Willemse	+	B	—	N	*
Catantopinae – Non-endemic genera						
Tarbaleus Brunner von Wattenwyl				M, NG		
	sp. n.	+	B	—	N	*
Oxya				Across		
	japonica japonica Thunberg	+	W	S, P	All	
	bolaangensis Hollis		W	—	N	*
	stresemanni Ramme		W	—	C	*
Gesonula				Across		
	mundata pulchra Rehn	+	W	S	N	
Chitaura				M, Java, India?		
	brachyptera Bolivar I	+	B	—	N	
	flavolineata (Willemse)		B	—	N	*
	atrata Ramme		B	—	C	*
	mirabilis Carl		B	—	C	*
	ochracea Ramme		B	—	S	*
	vidua Carl		B	M	S	
	mengkoka Ramme		B	—	SE	
	samanga Carl		B	—	S, SE, C	
	poecila Ramme		B	—	N	*
	elegans Ramme		B	—	S	*

Table 1. Species of Acridoidea occurring in Sulawesi and their distributions. (continued).

		Wings[1]	Distribution[2]		
			Outside	Within	
Oxytauchira			Burma		
	gracilis Willemse	W	—	C	*
Stenocatantops			Across		
	splendens Thunberg	+ W	Across	all	
	angustifrons Walker	W	Across	S	
Bibracte Stål			S, M, P		
	sp. n.	+ B	—	N	*
Valanga			Across		
	transiens Walker	+ W	—	N, C	
Oxyrrhepes			S		
	meyeri Willemse	W	—	?	*
	obtusa de Haan	W	S	N, C	
Cranaella			P		
	carnipes Ramme	B	—	N	*
Tristria			S		
	pisciforme Serville	W	S	N	
Austracris			P, A		
	guttulosa guttulosa Walker	W	A	N	
Mesambria			India?		
	maculipes Stål	+ B	—	all	
	elegans Ramme	B	—	S	
	trapezina Ramme	B	—	C	*
	rectangularis Ramme	B	—	N	*
Traulia			S, P, M		
	kukenthali Ramme	W?	—	?	*
	sanguinipes Stål	W?	S	?	
Apalacris			S, P		
	gracilis Willemse	W	—	S	
	incompleta Willemse	W	—	S	
	celebensis Willemse	W	—	?	*
Moessonia			NG		
	tenebrifera Walker	W?	—	N	

Notes
+ indicates a species collected by Project Wallace
1 – W – fully winged
    W? – winged but probably a poor flier
    B – brachypterous or wingless
2 – Distributions outside Sulawesi:
    M – Moluccas
    S – Sundaland
    P – Philippines
    A – Australasia
    NG – New Guinea
    Across – at least Sundaland to New Guinea

2 – Distributions within Sulawesi:
    all – all four regions
    N – North
    S – South
    SE – South-East
    C – Central

* indicates that the species is known only from one or a few sites.

are reasonably reliable since intensive collecting produced so few undescribed species, and those only from inaccessible habitats. Data on distribution within Sulawesi is less reliable with a significant proportion of species described from only one or a few localities. However collecting localities in the past have been widespread and so this may reflect very localised species distributions (see below). A probable exception is Central Sulawesi, parts of which remain very inaccessible. The expedition collection represents only a small proportion of the total acridoid fauna of Sulawesi (16 out of 59 described species) and this is also likely to be a result of localised species distributions rather than under-collecting.

The acridoid fauna of Sulawesi

Expedition and literature data give a total of 62 Sulawesi acridoid species in 33 genera and five subfamilies (table 1). The Catantopinae form by far the largest group with 53 species. This very diverse subfamily, which some authors consider to be an amalgam of several distinct subfamilies (eg Dirsh 1961), is one of the few acridoid groups to have adapted to forest environments. All of the non-

catantopine species in Sulawesi are forest edge or open habitat species whereas about 80% of catantopine species occupy habitats within the forest. Related to this is the occurrence of flightless species, with wings either absent or reduced, which are much more common in the Catantopinae (37/53 species) than in the other subfamilies (1/9 species). Flightlessness in grasshoppers is probably an adaptation to poor habitat quality, diversion of resources away from wing and flight muscle production allowing earlier reproduction and/or greater fecundity (Ritchie et al. 1987), and is common in forest species in other areas (Jago 1973).

Flightlessness clearly limits dispersal and so may have an impact on levels of endemism. In Sulawesi endemism is high for the Acridoidea, as it is for many other groups (Whitten et al. 1987) including Eumastacidae and Tetrigidae in the Orthoptera (Butlin et al 1989, Blackith & Blackith 1988). Overall 74% of acridoid species are endemic to Sulawesi but the proportion is higher in the Catantopinae (83%) than in the other subfamilies (22%). There is a clear link with the ability to fly: only two out of nine non-endemic catantopines are flightless, and the one flightless non-catantopine is endemic (table 1).

Table 2. Comparison of the Catantopinae of Sulawesi and Java.

	Java	Sulawesi
Number of species recorded	47	53
Number of genera recorded	34	24
Number of species per genus	1.38	2.21
Proportion of endemics – species	40%	83%
– genera	15%	33%

Table 3. Distributions outside Sulawesi.

	Non-endemic Species[1]	Non-endemic Genera[2]	Relationships of Endemic Genera[3]
Across	5	1 (10)	0
Sunda Shelf	7	4 (8)	2
Borneo (exclusively)	0	0 (0)	1
Philippines (exclusively)	1	1 (1)	0
Moluccas (exclusively)	1	0 (0)	0
Australasia	1	2 (3)	1

Notes

1. Includes distributions of *Oxya japonaci japonaci*, *Gesonula mundata pulchra*, and *Austracris guttulosa guttulosa*. All species have distributions 'Across' but the subspecies have informative distributions.
2. Excluding (including) genera with non-endemic species.
3. See text for details.

The special nature of the Sulawesi fauna can be appreciated better if it is compared with the fauna of Java. Java is the most comparable island in the region in terms of land area (126,500 km^2) but is part of the Sunda Shelf and has a clearly Oriental fauna. This comparison can be made most easily for the Catantopinae using data from C. Willemse (1956, 1957), F. Willemse (1965) and Hollis (1971, 1975). The total number of species recorded is similar (table 2) but the number of genera present in Sulawesi is lower with a significantly greater number of species per genus ($\chi^2 = 6.5$ P $<$ 0.01) Endemism at the species level in Sulawesi is twice that in Java, as is generic level endemism.

Biogeographical links

Sharing of taxa between Sulawesi and its surrounding areas is summarised in table 3 for non-endemic species (and subspecies) and genera. It is clear that Sulawesi shares the greatest number of species and genera with the Sunda Shelf as a whole (Peninsula Malaysia, Borneo, Sumatra, Java and Bali). This bias is strongest at the specific level but is also present among non-endemic genera. We have found no exclusive links with Borneo at either level, despite the close proximity of the two islands.

Links with the Philippines are mostly due to species or genera which also occur on the Sunda Shelf but there are two exclusive links, the gomphocerine *Eoscyllina luzonica* and the catantopine genus *Cranaella*. No species shared between Sulawesi and the Lesser Sunda Islands have been identified. To the east there is one species, *Chitaura vidua*, which occurs in Sulawesi and the Moluccas and one, *Austracris guttulosa*, which is distributed widely in Australasia and for which Sulawesi is the western limit. At the generic level there are two further links to the east, the genera *Moessonia* and *Tarbaleus*.

For endemic genera biogeographical information can only be derived from the distribution of sister genera but since the phylogeny of these groups has been studied very little these relationships are not known with any certainty. The following relationships, suggested by Ramme (1941) and Willemse (1951, 1956, 1957), are included in table 3. A group of four endemic genera, the Acrolophi (*Acrolophus, Alectorolophus, Alectorolophellus* and *Mengkokacris*), has apparently evolved within Sulawesi, indicating a long period of isolation. The nearest relatives of this generic group are apparently *Paralectorolophus* and *Lyrolophus* which occur on Lombok and Java respectively. The acridine genera *Calliphlaeoba* and *Phlaeobacris* are both probably related to *Phlaeoba* which has a Sunda Shelf plus Philippines distribution.

Heinrichius is believed to be most closely related to *Noliba* and therefore provides the only exclusive

link with Borneo. *Paracranae* is part of the *Cranae* group of genera which occurs in the Moluccas and New Guinea (Willemse 1977a, b).

Two genera are problematic because their nearest relatives are non-endemic Sulawesi genera. This implies that the latter are polyphyletic since the Sulawesi representatives of the two genera of each pair are likely to be more closely related to one another than the Sulawesi species of the non-endemic genus are to species in the same genus occuring elsewhere. *Celebesia* is believed to be most closely related to *Traulia* (Sulawesi and the Sunda Shelf), an *Paramesambria* to *Mesambria* (Sulawesi and India, Henry 1942). The distribution of *Mesambria* is particularly surprising but it is paralleled by *Chitaura* which also has an Indian representative (Hollis 1975). Neither of the two endemic genera (*Celebesia* and *Paramesambria*) has been included in table 3.

Endemism within Sulawesi

Mosaic distributions of species or subspecies within Sulawesi have been noted for several animal groups, eg macaques, carpenter bees, pond skaters (Whitten et al 1987 and see Knight & Holloway 1990). Ramme (1941) commented on a similar phenomenon in the Catantopinae and this appears quite striking when the island is divided into regions (table 4). A high proportion of the species present in any one region are known only from that region. This is particularly clear in the two most species rich genera in Sulawesi: *Alectorolophus* has nine species, seven of which are known from only one region, and *Chitaura* has ten species, nine of which are known from only one region. However the distributional information available is limited. Many species (table 1) are known from only one locality, but collecting localities overall have been widely distributed around the island and so this may represent genuinely very restricted distributions. Where more localities are known, five out of seven endemic and six out of eight non-endemic species are restricted to one region. Intensive searching of a restricted area during the Project Wallace expedition yielded only a small proportion of the total number of catantopine species known to occur in

Table 4. Regional distribution of Catantopine species within Sulawesi.

Region	Number of species occurring in:	
	that region only	that region and elsewhere
North	19	5
Central	8	6
South	12	5
South-East	3	5

Sulawesi (10/53) but a much higher proportion of the species known to occur in North Sulawesi (9/21). Only one species previously reported from another region was collected. Nine of the species not collected on the expedition were previously reported only from the western part of the peninsula of North Sulawesi, (particularly Toli-Toli) distant from the Dumoga-Bone National Park, suggesting that distributions are also restricted within regions. The within island endemism in the genus *Chitaura* is particularly striking in this context. Species in this genus are brightly coloured and conspicuous and occur on the forest edges as well as in light gaps within the forest. It is unlikely that the expedition would have failed to collect any species occurring in the Dumoga Bone area and yet only one of the ten Sulawesi species was found. This argument applies to collecting of *Chitaura* in general and so this genus gives strong support to the existence of intra-island endemism, and would be a good candidate for further work.

DISCUSSION

The Acrididae of Sulawesi show four main characteristics: (a) a high level of endemism, (b) low generic diversity but a high number of species per genus, (c) diverse distributions outside Sulawesi, and (d) localised species distributions within the island. These features have parallels in several other animal groups (Whitten et al 1987, Knight & Holloway 1989) and can be related to the geological history of the island.

The Acridoidea did not begin their radiation until the mid-Tertiary (Sharov 1968), that is after the break up of Gondwanaland and the beginning of the proposed northward movements of the fragments of present day Sulawesi. Thus the current Acridoid fauna of Sulawesi must have originated by dispersal and its low generic diversity can be explained in one of two ways: either Sulawesi was more isolated for much of its history than it is at present, or it has only recently become dry land due to tectonic uplift. The former explanation is more consistent with the observation of high levels of specific and generic endemism and high numbers of species per genus on the island, all of which suggest a long period of independent evolution for the Sulawesi acridoids. The sources of colonists for Sulawesi appear to have been numerous although the largest number of shared species and genera is clearly with the Sunda Shelf region. This may be partly due to the higher diversity of Acridoidea in Asia than in Australasia but there are several species or subspecies distributions which extend eastwards only as far as Sulawesi and very few equivalent Australasian distributions which extend westwards to Sulawesi. Thus at least a part of Sulawesi appears to have been closer to the Sunda Shelf than to Australasia for a significant

part of its history. However its current proximity to Borneo is probably recent since there are no exclusive biogeographical links at the level of shared species or genera. This is also true in other animal groups, notably the butterflies (Vane-Wright 1990). Exclusive links with the Philippines and Moluccas are also weak and may be recent. This is consistent with a general geological view of the area as a collision zone in which the area of dry land is increasing and land masses are moving closer together.

The high proportion of endemic species and genera in Sulawesi, the number of species per genus, and the evidence for evolution of new genera within the island all suggest not only a long period of isolation but also the opportunity for considerable evolutionary change and speciation. The mosaic distributions of species, particularly in the forest dwelling, flightless catantopines, may provide a clue to the conditions which have favoured these developments. Mosaic distributions are a feature of several other animal groups (Whitten et al 1987, Knight & Holloway 1990) and the patterns in different groups appear to be broadly coincident, defining areas of endemism within Sulawesi. The simplest explanation for these areas of endemism is past fragmentation of Sulawesi. This could have been in the form of an archipelago at times of higher sea level or before tectonic uplift and volcanic activity had created the present land mass (Musser 1987), or due to reduction in the extent of forest habitats in periods of drier climate (Morley & Flenley 1987). The wingless, forest adapted catantopines would be particularly susceptible to population fragmentation by such processes. Evolutionary divergence on islands or in refugia would have been followed by expansion to form the present mosaic distribution. Contact zones between the forms have not been studied, or indeed accurately located, and so the consequences of renewed contact are unknown. In general several possible types of interaction exist: sufficiently divergent forms may be able to spread into sympatry progressively obscuring the mosaic pattern, less divergent forms may interact at sharp parapatric boundaries due to ecological exclusion, or where reproductive isolation is incomplete a hybrid zone may form (Barton & Hewitt 1985). Identification and analysis of such contact zones is likely to be a very productive area for future research.

Strict isolation on islands or in refugia may not be necessary for evolutionary divergence (Barton 1989), especially in an island with the curious shape of Sulawesi in which gene flow between populations inhabiting different peninsulas would be extremely restricted even if they were connected by continuous suitable habitat. However,divergence without isolation is likely to produce different patterns of variation for individual characters within

species as well as for different species. Coincidences of patterns of variation are most likely to be produced by contraction and expansion of populations, and this process may be necessary for the completion of speciation (Hewitt 1989).

The mosaic distributions of species within Sulawesi constitute evidence either for the archipelagic nature of the land mass in the past or for habitat fragmentation during climatic fluctuations, or both. The time scale for these changes, and thus for the evolution of the Sulawesi endemics, is uncertain. They could have occurred mainly in the Pleistocene or over a much longer time scale of the order of the 15Myrs suggested as the time since the formation of Sulawesi as a single unit (Audley-Charles 1987). Most probably the present fauna of Sulawesi is the result of several superimposed periods of divergence. Studies of genetic divergence and detailed investigations of the contact zones appear to be the way forward in understanding the evolution of the Sulawesi grasshoppers.

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